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Hyrachyus, *Chasmoderium*, and the Early Evolution of Helaletid Tapiroids

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INTRODUCTION

One of the most common genera in collections of North American Middle Eocene fossil mammals is the medium-sized ceratomorph *Hyrachyus*. In the last revision of this group, Wood (1934) recognized it as a family, the Hyrachyidae, including 12 species allocated to four genera. My studies, based on larger samples than were available to Wood more than 30 years ago, suggest that recognition of no more than one genus and two species in North America is justified by the present evidence. The first part of this paper is a taxonomic revision of species of *Hyrachyus* from the Bridger Formation, which include most known *Hyrachyus* specimens. The Bridger Formation, Bridger Basin, Wyoming, contains two faunas, an earlier one from Bridger B beds and a later one from Bridger C and D beds (Matthew, 1909; Wood, 1934, p. 241); in the following discussion, *Hyrachyus* specimens are grouped accordingly. The second part of this paper deals with *Hyrachyus* from outside the Bridger Basin, including Eurasian forms, and the third part discusses the phylogenetic position of *Hyrachyus* and *Chasmoderium*.

The European genus *Chasmoderium* is included in this study, because two species formerly assigned to it, here transferred to *Hyrachyus*, provide

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a transitional sequence that links the aberrant genotypic species *Chasmotherium cartieri* to *Hyrachyus*.

Except for the dentition, little mention is made of the anatomy of *Hyrachyus*, because the skeleton of *Hyrachyus* closely resembles that of the Early Eocene ceratomorph *Heptodon*, which was recently described in detail (Radinsky, 1965a). All species of *Hyrachyus* are larger than *Heptodon* species, and the bones are correspondingly more robust but otherwise extremely similar.

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ABBREVIATIONS

A.M.N.H., the American Museum of Natural History
A.N.S.P., Academy of Natural Sciences of Philadelphia
C.M., Carnegie Museum, Pittsburgh
F.M.N.H., Field Museum of Natural History (formerly Chicago Natural History Museum)
P. U., Princeton University
U.S.N.M., United States National Museum, Smithsonian Institution, Washington
Y.P.M., Peabody Museum of Natural History, Yale University, New Haven
L, anteroposterior length (maximum)
W, labiolingual width (maximum)
mm., millimeters (all measurements are given in millimeters)
N, number of specimens included in sample
OR, observed range
M, mean
S, standard deviation
V, coefficient of variation

HYRACHYUS OF THE BRIDGER FORMATION

The characters used by Wood (1934) and earlier workers to distinguish genera and species within the *Hyrachyus* group are: size, differences in upper premolar cusp patterns, the presence or absence of rugose areas on the nasal bones, and the degree to which the upper molars approach the rhinocerotoid condition.

SIZE

On the basis of size, Wood (1934, p. 190) recognized four species of *Hyrachyus* from the Bridger Formation: *H. affinis*, length $M^{1-3}=43-46$ mm.; *H. modestus*, $M^{1-3}=49-57$ mm.; *H. eximus*, $M^{1-3}=60-67$ mm.; and *H. princeps*, $M^{1-3}=66-72$ mm. Specimens from both the lower (B beds) and upper (C and D beds) Bridger faunas were assigned to *H. affinis*; *H. modestus* was confined to Bridger B beds, and *H. eximus* and *H. princeps* were recognized only in Bridger C and D beds. However, the data now available suggest that probably only a single species is present in the early fauna and only two species in the later fauna. These conclusions are particularly evident when the frequency distributions of the lengths of the lower molar series, in addition to those of the uppers, are considered (see fig. 1). For the Bridger B sample the frequency histogram of length M_{1-3} approximates a normal unimodal distribution curve. One specimen, F.M.N.H. No. UC1732, is discontinuously larger than the rest of the sample ($M_{1-3}=67$ mm.). The distribution of M^{1-3} length is slightly bimodal for the main part of the sample, and two specimens are discontinuously large (Y.P.M. No. 10258, $M^{1-3}=63$ mm., and U.S.N.M. No. 23642, $M^{1-3}=65$ mm.). The bimodality, in my opinion, is not marked enough to support recognition of two species; it may reflect a sexual dimorphism not evident in the lower teeth or a sampling artifact. In any event, with the exception of the three large specimens mentioned above, all Bridger B *Hyrachyus* specimens fall within the size range one might expect for a single species, especially when the sample is not from a single quarry (see table 1). Y.P.M. No. 10258 and U.S.N.M. No. 23642 fall between the 95 and 99 per cent confidence limits of the sample, but the lower dentition, F.M.N.H. No. UC1732, falls outside 3 standard deviations from the sample mean. If the stratigraphic datum for the lower dentition is correct, it suggests that a large species of *Hyrachyus* existed during early Bridgerian time.

The *Hyrachyus* sample from the upper Bridger beds (C-D) falls into two size groups, one averaging about 10 per cent smaller than the Bridger B mean, and the other 20 per cent larger. Two upper dentitions, Y.P.M.

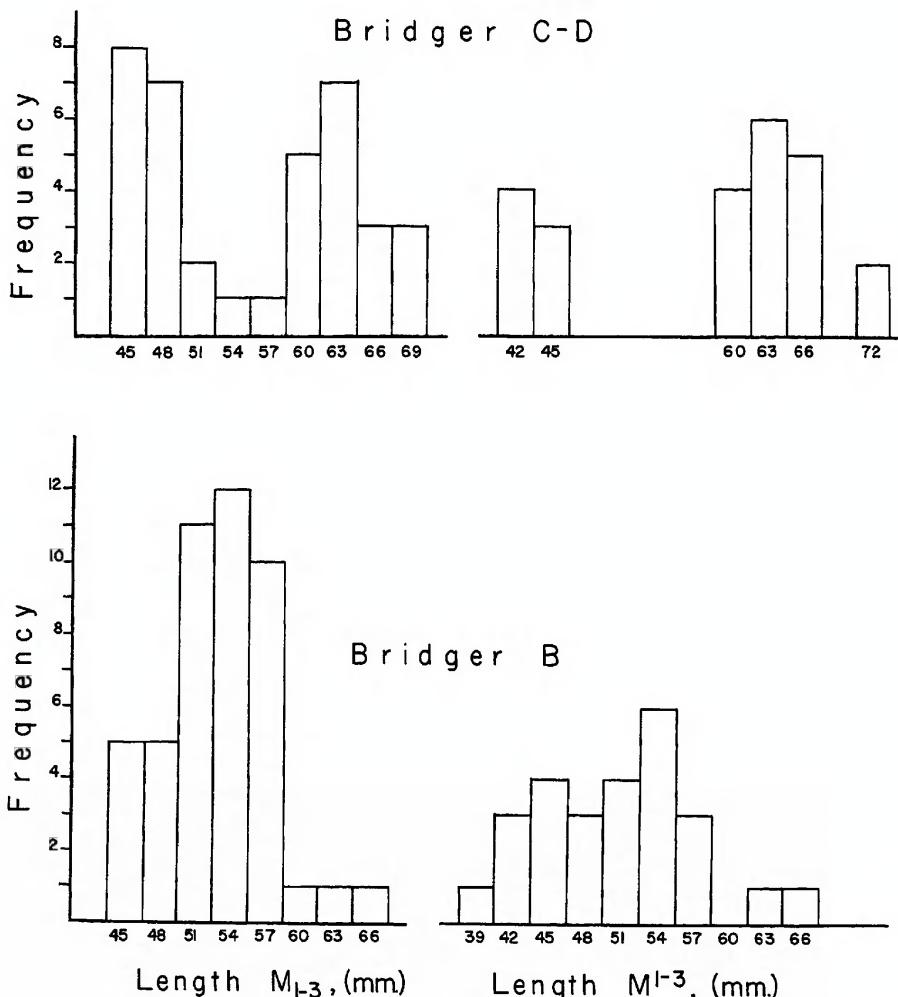


FIG. 1. Frequency distribution histograms of lengths of upper and lower molar series of *Hyrachys* specimens from Bridger B beds and Bridger C and D beds.

No. 11157 (the type of *H. princeps*) and A.M.N.H. No. 12364, are discontinuously larger than the other large specimens, but, when all the large upper dentitions are treated statistically as a single sample, the coefficient of variation for the length of M^{1-3} is as low as one would expect for a single species (see table 3). Also, the large lower dentitions provide no good evidence for recognition of more than one species. It is interesting that the difference in size between the small and large Bridger C-D *Hyrachys* specimens is apparently more marked in the upper dentitions than in the lowers. This fact may be correlated with the suggestion of

bimodality in the Bridger B upper molars, compared with the unimodal curve of the Bridger B lower dentitions. In other words, the upper molars may be more sensitive indicators of size differences than the lowers.

To sum up, the data on size (based on tooth dimensions) indicate the presence of a single medium-sized species of *Hyrachyus* in the Bridger B beds, and two species, one smaller and the other larger, in the upper Bridger beds. Student's *t*-tests indicate that the differences between the means of the three samples are significant above the 99 per cent level. In other words, the chances are less than one in 100 that any two of the samples were drawn from the same population, which does not mean, however, that three different species are represented. The formal classification of these *Hyrachyus* samples is discussed below, after a consideration of the other taxonomic criteria that have been used.

OTHER TAXONOMIC CRITERIA

Wood (1934, p. 205) erected the species *Hyrachyus hypostylus* for a single large late Bridgerian specimen, A.M.N.H. No. 12666, in which an accessory cuspule, called a hypostyle, is present posterior to the metaloph on the right P^{3-4} . The left P^4 , however, shows only the barest trace of this feature. The presence of extra cuspules is a not uncommon individual variation in many species of Eocene perissodactyls, and, except for this extra cuspule, A.M.N.H. No. 12666 differs in no significant way from the rest of the large late Bridgerian *Hyrachyus* sample. Therefore I see no reason for recognizing it as a distinct species.

Two specimens, which in size and molar cusp pattern are indistinguishable from the large late Bridgerian *Hyrachyus* species, have an unusual premolar cusp pattern: a large transverse crest, apparently homologous with a metaloph, is present on P^2 ; in one specimen, Y.P.M. No. 10258, it is the only transverse crest, whereas in A.M.N.H. No. 12362, there is a small protoconule. In addition, P^3 of A.M.N.H. No. 12362 and P^{3-4} of Y.P.M. No. 10258 show incipient separation of hypocone from protocone. The latter specimen includes nasal bones which bear small rugose thickenings, and on the basis of that feature and the precocious P^{3-4} , Troxell (1922, p. 33) made Y.P.M. No. 10258 the type of a new genus and species, *Metahyrachyus bicornutus*. Wood (1934, p. 226) considered the unusual P^2 the most important diagnostic character of *Metahyrachyus*, and erected a second species, *M. troxelli*, for A.M.N.H. No. 12362.

Normally in *Hyrachyus* the protoloph is the dominant cross crest on the premolars, but the condition seen in the two specimens described above is approached in P^2 's of A.M.N.H. Nos. 11660, 12360 and, to a lesser degree, A.M.N.H. No. 12666 (all three are large late Bridgerian speci-

TABLE 1
STATISTICAL DATA ON TEETH OF *Hyrachys modestus* FROM BRIDGER B BEDS

	N	O.R.	M	S	V
P ¹					
L	12	7.1-9.5	8.67±0.19	0.66	7.61
W	12	4.9-7.0	6.17±0.17	0.59	9.56
P ²					
L	15	7.2-11.1	9.27±0.26	1.01	10.90
W	15	7.8-12.4	10.40±0.36	1.40	13.46
P ³					
L	19	9.0-12.4	10.64±0.23	0.98	9.21
W	19	10.5-16.4	14.16±0.42	1.81	12.78
P ⁴					
L	22	9.7-14.6	12.13±0.32	1.51	12.45
W	22	13.8-19.4	16.49±0.40	1.88	11.40
M ¹					
L	23	12.3-18.0	15.54±0.35	1.69	10.95
W	23	14.9-21.4	18.68±0.38	1.80	9.64
M ²					
L	24	14.0-20.2	17.50±0.39	1.90	10.86
W	24	16.3-23.7	20.53±0.43	2.12	10.33
M ³					
L	26	13.8-20.2	17.43±0.36	1.82	10.44
W	26	16.4-24.8	20.21±0.44	2.22	10.98
LP ¹⁻⁴	16	33 -50	41.50±1.16	4.65	11.20
LM ¹⁻³	24	40 -57	49.29±1.11	5.43	11.02
P ₁					
L	7	6.0- 8.5	7.24±0.30	0.80	11.05
W	7	4.0- 5.0	4.24±0.15	0.40	9.43
P ₂					
L	15	8.8-11.9	9.77±0.21	0.80	8.19
W	15	5.4- 7.7	6.15±0.16	0.63	10.24
P ₃					
L	28	9.8-14.4	11.95±0.24	1.26	10.54
W	28	6.0-10.5	8.05±0.21	1.13	14.04
P ₄					
L	42	10.9-15.0	13.12±0.19	1.23	9.38
W	42	6.7-11.2	9.26±0.16	1.06	11.45
M ₁					
L	43	13.0-20.2	16.00±0.24	1.55	9.69
W	43	9.0-13.2	11.10±0.16	1.05	9.46
M ₂					
L	45	14.3-21.8	18.09±0.26	1.74	9.62
W	45	9.8-14.0	12.30±0.16	1.05	8.54
M ₃					
L	35	16.2-22.8	19.58±0.27	1.58	8.07
W	35	10.0-15.0	12.65±0.20	1.16	9.17
LP ₁₋₄	15	36-50	41.20±0.90	3.47	8.42
LM ₁₋₃	45	44-62	52.53±0.65	4.33	8.24

TABLE 2
STATISTICAL DATA ON TEETH OF *Hyrachys modestus* FROM BRIDGER C AND D BEDS

	N	O.R.	M	S	V
P ¹					
L	2	7.7-8.0	7.85		
W	2	4.1- 4.1	4.10		
P ²					
L	2	7.4- 8.5	7.95		
W	2	7.4- 7.8	7.60		
P ³					
L	3	9.2-11.0	9.90		
W	3	11.5-11.9	11.77		
P ⁴					
L	4	10.7-11.5	11.05		
W	4	13.8-14.9	14.30		
M ¹					
L	3	12.9-13.6	13.20		
W	3	14.3-17.1	15.77		
M ²					
L	5	14.7-15.7	15.00±0.18	0.40	2.67
W	5	16.1-18.3	17.26±0.44	0.99	5.74
M ³					
L	10	14.5-17.0	15.31±0.27	0.84	5.49
W	10	15.9-20.4	17.31±0.42	1.33	7.68
LP ¹⁻⁴	3	35-37	36.00		
LM ¹⁻³	7	41-45	43.14±0.55	1.45	3.36
P ₁					
L	0				
- W	0				
P ₂					
L	3	7.2-10.2	8.67		
W	3	4.4- 6.2	5.20		
P ₃					
L	7	8.9-11.8	10.19±0.35	0.92	9.03
W	7	5.4- 8.2	6.69±0.36	0.94	14.05
P ₄					
L	13	10.2-13.4	11.72±0.22	0.81	6.91
W	13	6.8- 9.7	8.15±0.25	0.89	10.92
M ₁					
L	16	12.7-15.8	13.98±0.20	0.81	5.79
W	16	8.2-12.3	9.27±0.25	1.01	10.90
M ₂					
L	14	14.2-18.5	15.94±0.29	1.10	6.90
W	14	9.7-13.1	10.66±0.29	1.07	10.04
M ₃					
L	12	16.1-19.0	17.45±0.20	0.73	4.18
W	12	9.7-11.7	10.53±0.20	0.69	6.55
LP ₁₋₄	5	32-37	35.20±0.86	1.92	5.45
LM ₁₋₃	19	44-54	47.05±0.60	2.62	5.57

mens). In addition, incipient separation of hypocone from protocone is seen in P⁴ of A.M.N.H. No. 11651 (early Bridgerian) and A.M.N.H. No. 11446 (large late Bridgerian). These kinds of premolar variations are common in Eocene perissodactyls (see for example Radinsky, 1963, pp. 15, 20, and 47; and Gazin, 1962, pl. 13) and, in the absence of more significant characters, do not appear to be indicative of species differentiation. The nasal rugosities of *Metahyrachys bicornutus* (see Troxell, 1922, fig. 4) are very slight thickenings on the posterior part of the nasals which would not be noticeable except for the radiating pattern of striations on the bone surface. Most *Hyrachys* specimens that preserve the nasals are cracked in that area so that it is not possible to determine how much variation existed in that feature. In any event, it seems too minor a character, even in conjunction with the unusual premolar pattern, to justify even species-level recognition. Since *Metahyrachys bicornutus* and *M. troxelli* are otherwise indistinguishable from *Hyrachys* species, I see no compelling reason to maintain them as separate taxa. The type of *M. troxelli* is from late Bridgerian beds and fits in well with the large *Hyrachys* species in those strata. Locality information with Y.P.M. No. 10258, however, suggests a Bridger B horizon, and Y.P.M. No. 10258, along with two other specimens (see above), falls outside the observed size of the Bridger B *Hyrachys* sample. Nevertheless it does fall within the predicted 99 per cent size limits of the early Bridgerian species.

Marsh (1873, p. 407) proposed a new genus and species, *Colonoceras agrestis*, for Y.P.M. No. 11082, an almost complete skull from an unknown level in the Bridger Formation. Both Troxell (1922, p. 33) and Wood (1934, p. 225) considered its generic separation from *Hyrachys affinis* as tenuous, but nevertheless maintained it as a distinct genus. Wood (*ibid.*, p. 223) listed as generic characters for *Colonoceras* its progressive upper premolars and nasal rugosities. The premolars of Y.P.M. No. 11082 have metalophs (or metaconules) that are higher than those in most, but not all, *Hyrachys* specimens (see for example A.M.N.H. Nos. 5072 and 11651 from Bridger B beds and A.M.N.H. No. 12359 from the upper Bridger beds). *Colonoceras agrestis* appears to represent merely one extreme in a spectrum of continuous variation in premolar pattern. The nasal rugosities on Y.P.M. No. 11082 (figured in Troxell, 1922, figs. 1 and 2) are situated slightly more anteriorly and are slightly thicker than those of Y.P.M. No. 10258 ("*M. bicornutus*"), but again are noticeable primarily because of the bone surface pattern. Since Y.P.M. No. 11082 otherwise falls within the morphological range of small *Hyrachys* specimens, and since nothing is known of the range of variation of the nasal rugosities (a minor difference at most), I see no good reason for maintaining *Colono-*

ceras agrestis as a distinct species.

Wood (1934, p. 232) proposed a new genus, *Ephyrachyus*, for A.M.N.H. No. 5078, the type of *Hyrachyus implicatus* Cope, 1873. A.M.N.H. No. 5078 is from the Washakie Formation, from which *Hyrachyus* is unknown, and falls within the range of variation of a species of the hyracodontid rhinocerotoid *Triplopus* which is found in the same beds. For these reasons I have recently transferred *E. implicatus* to *Triplopus* (see Radinsky, 1967, p. 9). Wood (1934, p. 238) proposed a second species of *Ephyrachyus*, *E. cristalophus*, for a Bridger C specimen, A.M.N.H. No. 12359, which he considered to differ from *Hyrachyus* in having more rhinocerotoid-like upper molars and a peculiar P^4 pattern. The unusual feature about the P^4 of A.M.N.H. No. 12359 is that the crista extends to the metaconule, forming a small fossa. However, this is merely an individual variation of the kind occasionally seen in Eocene perissodactyl premolars and is not a good specific character. The molars of A.M.N.H. No. 12359 are slightly relatively higher-crowned than are those of most *Hyrachyus* specimens, a fact that I believe is responsible for the more progressive appearance of those teeth. However, this feature is common to all small late Bridgerian *Hyrachyus* specimens and also to most of the smaller Bridger B *Hyrachyus* specimens. Therefore I can see no valid reasons for separating *E. cristalophus* generically from *Hyrachyus*.

CONCLUSIONS

Of all the characters used to diagnose genera and species within the *Hyrachyus* group from the Bridger Formation, only size appears to be a useful and valid taxonomic criterion. On the basis of molar series length, three size classes are evident: a medium-sized one in the early Bridger fauna and smaller and larger-sized groups in the late Bridger fauna. At least two, and at most three, species are suggested by the data. The large late Bridger form averages 20 per cent larger than the early Bridgerian one, and 25 per cent larger than the small late Bridgerian form, and therefore may be considered to represent a distinct species. However, there is only a 10 per cent difference between the mean of the molar series length of the early Bridgerian form and that of the small late Bridgerian form, with the range of the latter completely overlapped by that of the former. As the two samples are statistically separable, one could argue for recognition of the difference on the specific or subspecific level. However, because the mean size difference is so small and because there are no other known features that separate the two groups, I propose to place them in the same species. Only the trinomial remains, therefore, for possible taxonomic reflection of the size difference, but, be-

TABLE 3
STATISTICAL DATA ON TEETH OF *Hyrachys eximus* FROM BRIDGER C AND D BEDS

	N	O.R.	M	S	V
P ¹					
L	5	9.4-11.2	10.18±0.35	0.78	7.66
W	5	7.2- 9.3	8.00±0.36	0.81	10.13
P ²					
L	11	9.4-13.3	10.99±0.33	1.11	10.10
W	11	12.1-17.6	14.05±0.51	1.68	11.96
P ³					
L	15	10.6-16.0	13.06±0.31	1.20	9.19
W	15	14.7-23.8	19.15±0.58	2.26	11.80
P ⁴					
L	18	13.6-18.5	15.62±0.30	1.28	8.19
W	18	19.8-25.2	22.16±0.38	1.63	7.36
M ¹					
L	18	17.4-21.4	19.07±0.28	1.18	6.19
W	18	21.9-26.9	23.92±0.43	1.81	7.57
M ²					
L	19	20.7-25.4	22.63±0.33	1.44	6.36
W	19	23.0-31.0	26.97±0.51	2.22	8.23
M ³					
L	21	21.3-26.8	23.01±0.31	1.43	6.21
W	21	23.1-31.0	26.46±0.39	1.79	6.76
LP ¹⁻⁴	10	42-56	48.40±1.14	3.60	7.44
LM ¹⁻³	17	60-73	64.35±0.90	3.71	5.77
P ₁					
L	5	7.4- 8.8	7.64±0.37	0.83	10.86
W	5	4.1- 6.0	4.86±0.31	0.70	14.40
P ₂					
L	7	9.7-13.0	10.86±0.40	1.07	9.85
W	7	6.0- 8.5	7.27±0.36	0.94	12.93
P ₃					
L	7	11.5-15.7	13.11±0.55	1.45	11.06
W	7	8.3-11.5	9.63±0.42	1.12	11.63
P ₄					
L	11	12.9-18.1	14.95±0.45	1.49	9.97
W	11	9.4-13.9	11.27±0.36	1.21	10.74
M ₁					
L	19	15.7-21.8	18.63±0.36	1.58	8.48
W	19	11.0-15.1	13.07±0.24	1.03	7.88
M ₂					
L	17	19.6-25.3	22.01±0.39	1.61	7.31
W	17	13.2-17.2	14.89±0.24	0.97	6.51
M ₃					
L	20	20.0-28.4	24.35±0.45	1.99	8.17
W	20	13.0-18.6	15.45±0.27	1.22	7.90
LP ₁₋₄	7	43-50	47.29±0.98	2.60	5.50
LM ₁₋₃	19	58-70	63.58±0.89	3.87	6.09

cause so little is known of these animals other than the teeth, I prefer not to use subspecific names. Therefore, while recognizing the deficiency in terms of information content, I suggest using the same name for the small late Bridgerian form as for the early Bridgerian one.

Names that have been applied to the Bridger B *Hyrachyus* sample include: *Lophiodon modestus* Leidy, 1870; *Hyrachyus agrestis* Leidy, 1871; *Hyrachyus agrarius* Leidy, 1871; *Lophiodon bairdianus* Marsh, 1871; and *Metahyrachyus bicornutus* Troxell, 1922. The small late Bridgerian *Hyrachyus* sample includes the types of: *Hyrachyus crassidens* Osborn, Scott, and Spier, 1878; *Ephyrachyus cristalophus* Wood, 1934; and probably *Colonoceras agrestis* Marsh, 1873. The type of *Lophiodon modestus* Leidy, 1870, is U.S.N.M. No. 661, an isolated DP³ or DP⁴. It is unfortunate that this species name, which has priority over all the others, is based on such a poor specimen. However, since the generic and specific affinities of U.S.N.M. No. 661 are unmistakable, I follow Wood (1934, p. 191) in selecting *Hyrachyus modestus* (Leidy), 1870, as the correct name for this species.

The large-sized *Hyrachyus* specimens from the late Bridgerian fauna have received the following species names: *Hyrachyus eximius* Leidy, 1871; *Hyrachyus princeps* Marsh, 1872; *Hyrachyus imperialis* Osborn, Scott, and Spier, 1878; *Hyrachyus hypostylus* Wood, 1934; and *Metahyrachyus troxelli* Wood, 1934. The type of *Hyrachyus eximius* is A.N.S.P. No. 10320, a jaw fragment with P₄-M₁. Because it unquestionably belongs to the species under consideration, *H. eximius* Leidy, 1871, must stand as the valid name for this species.

The appearance of *Hyrachyus eximius* in the late Bridgerian fauna coincides with a decrease in the mean size of *H. modestus*. The simplest explanation of this occurrence is character displacement, if it be assumed that the smaller *H. modestus* individuals are subject to less competition from *H. eximius*. At present this kind of speculation is mainly an exercise in imagination, but with more information on Middle Eocene *Hyrachyus* populations it may become possible to verify such hypotheses.

HYRACHYUS FROM OUTSIDE THE BRIDGER BASIN

NORTH AMERICA

A small number of *Hyrachyus* specimens, indistinguishable from the early Bridgerian *H. modestus*, have been found at several late Early Eocene localities. These occurrences have been noted by Wood (1934, p. 197) for the Lost Cabin beds, Wind River Formation, Wind River Basin, Wyoming; Morris (1954, p. 201) for the Cathedral Bluffs member, Wasatch Formation, Washakie Basin, Wyoming; Gazin (1962, p. 80) for the New

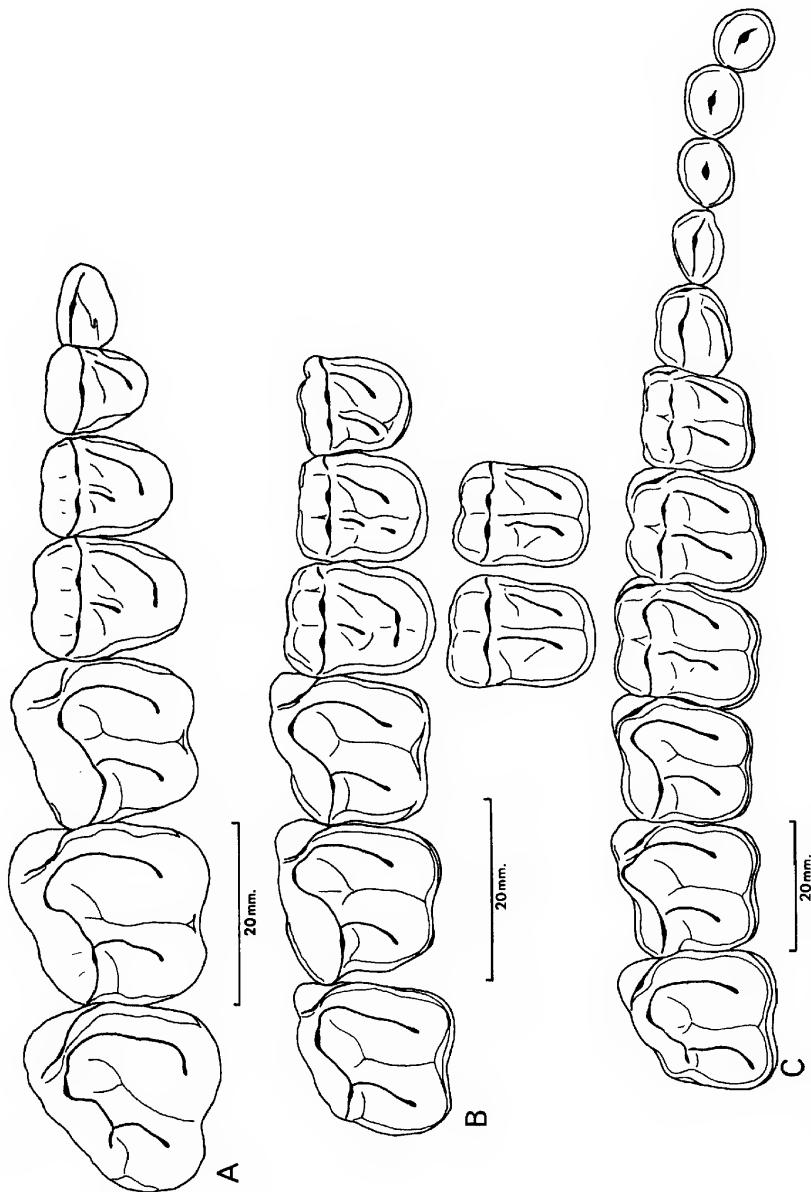


FIG. 2. Upper dentitions. A. Bridger B *Hyrachyus modestus*, A.M.N.H. No. 126667, P^1 - M^3 . B. *Hyrachyus minimus*, composite based on isolated teeth from Argenton, France, P^2 - M^3 , and advanced variants of P^{3-4} . C. *Chamaotherium cartieri*, composite based on several specimens, I^1 - M^3 .

Fork tongue of the Wasatch Formation, Green River Basin, Wyoming; and Robinson (1966, p. 67) for the upper faunal level (which may be early Bridgerian in age) of the Huerfano Formation, Huerfano Basin, Colorado. These are the oldest known occurrences of *Hyrachyus* in North America.

The supposed presence of *Hyrachyus* in the Washakie Formation, Washakie Basin, Wyoming, has been noted in several papers. For all such records that I have examined, I have found either the locality data dubious or the specimen misidentified. Primitive species of the hyracodontid rhinocerotoid *Triplopus* in the Washakie Formation are easily confused with *Hyrachyus*, especially if the M^3 is lacking (see Radinsky, 1967, p. 12).

Hyrachyus grandis Peterson, 1919, is based on a lower jaw from the lower part of the Uinta Formation, Uinta Basin, Utah. Recently discovered upper dentitions of this species indicate that it is a primitive hyracodontid rhinocerotoid, and I have assigned it provisionally to *Forstercooperia* (Radinsky, 1967, p. 25).

The anterior part of a skull with worn P^{1-4} and P_2-M_3 (C.M. No. 784), from the Late Eocene Sage Creek beds, Montana, is the type of *Hyrachyus?* *priscus* Douglass, 1902, renamed *Hyrachyus douglassi* by Wood (1934, p. 208). A few lower dentitions and one deciduous upper dentition from the Uinta B beds, Uinta Formation, Utah, were referred to *H. douglassi* by Wood (1934, p. 209). C.M. No. 784 and the Uinta Formation specimens (A.M.N.H. No. 1929; C.M. Nos. 2940 and 3112; P.U. Nos. 11289 and 11292) represent a species about the size of *Hyrachyus eximius*, but without the M^3 or unworn upper molars it is not possible to determine whether they represent *Hyrachyus* or the primitive hyracodontid *Triplopus*. A small species of *Triplopus*, *T. obliquidens*, occurs in the Uinta B beds (see Radinsky, 1967, p. 13), and, as Eocene perissodactyl genera are commonly represented by small and large species in a given fauna, it is quite possible that *Hyrachyus douglassi* actually belongs to *Triplopus*. However, until a good upper dentition of *H. douglassi* is discovered, its generic affinities will remain open to question.

EUROPE

Savage, Russell, and Louis (1966, p. 2) transferred to *Hyrachyus* the primitive Cuisian (=late Early Eocene) ceratomorph *Chasmotherium stehlini* Deperet, 1904. After examining all available specimens of *H. stehlini*, I agree with their conclusion that the species in question is more properly referred to *Hyrachyus* than to the aberrant tapiroid *Chasmotherium*. However, their formal species diagnosis did not diagnose it, for it merely stated that *H. stehlini* was the same size as small North American *Hyra-*

TABLE 4
STATISTICAL DATA ON TEETH OF *Hyrachyus modestus* FROM THE CUISIAN OF EUROPE

	<i>N</i>	O.R.	<i>M</i>
P ¹	0		
P ²	0		
P ³			
L	1		9.0
W	1		12.5
P ⁴			
L	2	10.9-12.1	11.50
W	2	13.8-15.5	14.65
M ¹			
L	3	11.8-14.2	13.33
W	3	14.6-16.9	16.03
M ²			
L	5	13.9-16.5	15.86
W	5	16.0-18.2	17.32
M ³			
L	8	14.3-16.3	15.19
W	8	15.6-17.7	16.75
LM ¹⁻³	3	40-46	43
P ₁	0		
P ₂			
L	1		8.8
W	1		5.5
P ₃			
L	3	9.8-10.3	10.00
W	3	5.9- 7.4	6.57
P ₄			
L	2	10.2-10.7	10.45
W	2	7.4- 7.8	7.60
M ₁			
L	5	12.7-14.0	13.26
W	5	8.6- 9.2	8.86
M ₂			
L	7	14.3-16.2	15.03
W	7	9.8-10.6	10.13
M ₃			
L	5	15.8-16.5	16.08
W	5	9.8-10.6	10.26
LM ₁₋₃	4	43-45	44

chys species. In known morphology, which is primarily dental, *H. stehlini* falls within the range of variation of *H. modestus*, and, had the European specimens been found in the Bridger Basin, they surely would not have been placed in a separate species. *Hyrachyus stehlini* can be distin-

guished from *H. modestus* only on the basis of its locality data, which are not sufficient justification for taxonomic separation. Therefore, until morphological differences between the European and North American forms can be demonstrated, I place *H. stehlini* in synonymy with *H. modestus*. Statistics on dental measurements, based on a larger sample than was listed in Savage, Russell, and Louis (1966), are given in table 4.

A more difficult problem lies in assessing the taxonomic position of the Lutetian (= Middle Eocene) species *Chasmotherium minimum* (Fischer), 1829, (see fig. 2). *Chasmotherium minimum*, known primarily from a collection of isolated teeth from Argenton, France, differs from European *Hyrachys modestus* (*H. "stehlini"*) in being about 10 per cent larger and in the following dental features: lingual cingula usually present on upper molars and premolars; upper molar metacones with stronger labial cingula; M^3 metacone shorter; premolars more molariform. In these features *Chasmotherium minimum* is intermediate between the European *H. modestus* sample and *Chasmotherium cartieri* Rütimeyer, 1862. The latter species, type of the genus *Chasmotherium*, is based on specimens from Lutetian fissure fillings at Egerkingen, Switzerland, and known also from deposits at Buchsweiler, Switzerland, and Lissieu and Robiac, France. *Chasmotherium cartieri* further differs from *Hyrachys modestus* in lacking a diastema between canines and cheek teeth, and in having conical, pointed incisors. The incisors and canines are unknown in *C. minimum*. Savage, Russell, and Louis (1966, p. 14) stated that Filhol's (1888, pl. 9, figs. 6 and 7) illustrations of the only known mandible of *C. minimum* (broken just in front of P_1) suggest a small or no postcanine diastema, but I cannot determine that from the illustration and have not seen the original specimen.

European *Hyrachys modestus*, *Chasmotherium minimum*, and *C. cartieri* form a gradational morphological series, with *H. modestus* and *C. cartieri* different enough to justify generic separation. However, it is an arbitrary matter as to where the generic boundary should be drawn with respect to *C. minimum*. On the basis of the cheek teeth alone, I agree with Savage, Russell, and Louis (1966, p. 15) that *C. minimum* is closer to *Hyrachys modestus* than to *Chasmotherium cartieri*, and therefore transfer it to the former genus. If future discoveries show the anterior dentition of *Hyrachys minimus* (emended spelling) to be more similar to that of *C. cartieri* than *H. modestus*, then I would reassign it to *Chasmotherium*. Dental measurements of *H. minimus* are summarized in table 5.

Fischer (1964, p. 48) described an excellent collection of *Hyrachys* specimens from the Geiseltal brown coals, near Halle, German Democratic Republic, under the name *Chasmotherium minimum* (in which Fischer included *C. stehlini*). The Geiseltal specimens come from two levels in the

TABLE 5
STATISTICAL DATA ON TEETH OF *Hyrachys minimus* FROM ARGENTON, FRANCE

	N	O.R.	M
P ¹			
L	1		10.0
W	1		7.9
P ²			
L	3	10.1-10.8	10.46
W	3	11.7-11.9	11.70
P ³			
L	2	11.3-11.4	11.35
W	2	14.6-14.6	14.60
P ⁴			
L	4	11.8-12.5	12.18
W	4	15.8-16.7	16.18
M ¹			
L	2	15.2-15.4	15.30
W	2	16.5-16.8	16.65
M ²			
L	3	17.0-18.7	17.77
W	3	18.2-19.4	18.63
M ³			
L	7	16.5-18.0	17.34
W	7	18.2-19.5	18.57
P ₁	0		
P ₂			
L	3	10.4-11.9	11.17
W	3	6.5- 7.3	6.90
P ₃			
L	3	11.8-12.4	12.13
W	3	8.5- 9.1	8.80
P ₄			
L	7	12.8-13.7	13.29
W	7	8.2-10.2	9.36
M ₁			
L	5	14.5-15.7	15.30
W	5	9.8-10.5	10.18
M ₂			
L	6	15.9-18.7	17.03
W	6	11.2-11.9	11.48
M ₃			
L	5	16.8-19.6	18.16
W	5	11.0-12.3	11.54
LM ₁₋₃	1		49

coal beds, but appear to represent a single species which is about the size of the Argenton *H. minimus*, but not quite so advanced in cheek tooth morphology, i.e., lingual cingula weaker, cingula labial to molar metacones weaker, premolars less molariform. However, these features vary within the Geiseltal sample, and some individuals (not necessarily from the higher levels) are about as advanced as some Argenton *H. minimum* specimens. The Geiseltal form has a postcanine diastema and spatulate incisors.

The Geiseltal *Hyrachyus* specimens bridge the gap in cheek tooth morphology between *H. modestus* and *H. minimus*, and the absence of any sharp morphological discontinuities makes allocation to one species rather than to the other a subjective matter. The dentition of the Geiseltal form appears to me to be slightly closer to that of *H. modestus*, and I therefore assign it to that species. I do believe that there is enough morphological difference between *H. modestus* and *H. minimus* to justify specific recognition.

An uncrushed and almost complete skull of the Geiseltal *H. modestus*, Halle No. 22/439, resembles Bridger Basin *Hyrachyus* skulls except for one feature: on both sides it lacks an alisphenoid canal. A groove in the alisphenoid bone marks the passage of the internal maxillary artery, but there is no indication that it was ever walled over by bone. This condition is unexpected; all other perissodactyls I know of, including the Early Eocene genera *Hyracotherium*, *Homogalax*, and *Heptodon*, have an alisphenoid canal. The absence of ossification lateral to the internal maxillary artery in Halle No. 22/439 may be an individual abnormality, or may represent the general condition of the Geiseltal *Hyrachyus* population. Even if the latter possibility should prove to be true, that distinction alone would not, in my opinion, merit formal taxonomic recognition.

Atalonodon Dal Piaz, 1929, known only from a lower jaw from Lutetian beds in Sardinia, was tentatively referred to *Hyrachyus* by Savage, Russell, and Louis (1966, footnote, p. 36). In known anatomy *Atalonodon* resembles *Hyrachyus* in lacking an M_3 hypoconulid, but differs from that genus in having a larger canine, no P_1 , and a more posteroventrally projecting angular process. These differences suggest that *Atalonodon* is generally distinct from *Hyrachyus*. Knowledge of the upper dentition of *Atalonodon* is needed to determine its phylogenetic relationships.

ASIA

I recently (Radinsky, 1965b, p. 234) described a maxilla with P^4-M^3 from probably early Late Eocene beds in Inner Mongolia, which closely resembles comparable parts of *Hyrachyus*. However, since the molars of *Hyrachyus* are not much changed from the primitive ceratomorph condi-

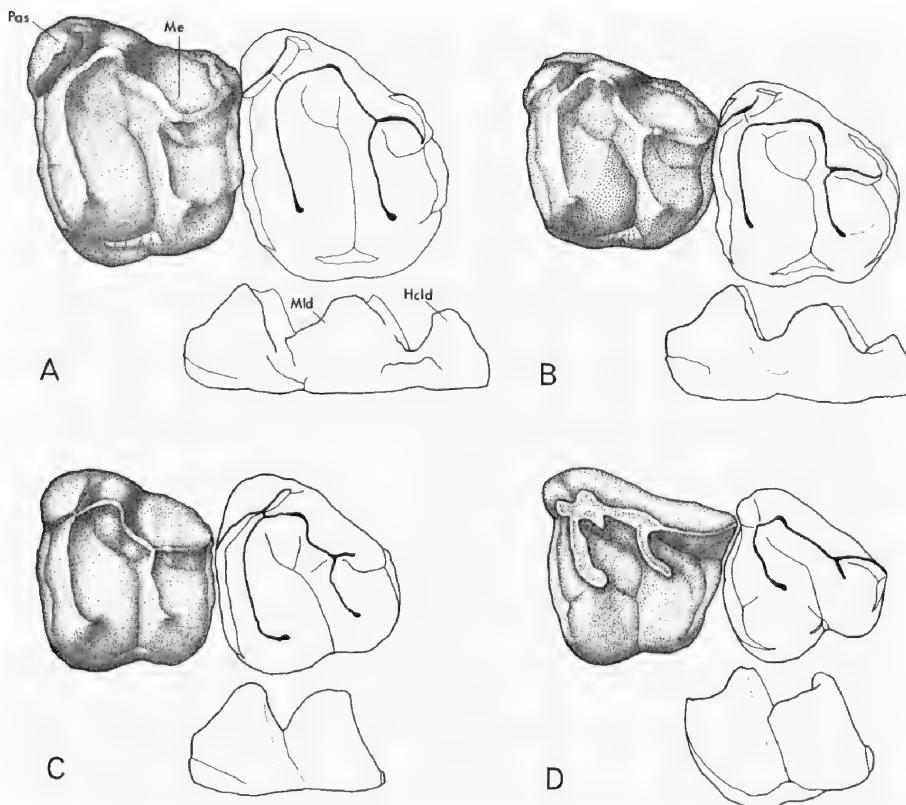


FIG. 3. M^{2-3} , crown view, and M_3 , lateral view. A. *Heptodon calciculus*. B. *Helaletes nanus*. C. *Hyrachyus modestus*. D. *Hyracodon nebrascensis*, representing a rhinocerotoid pattern. A and B are drawn to twice the scale of C and D. From Radinsky (1966a).

Abbreviations: Hcld, hypoconulid; Me, metacone; Mld, metalophid; Pas, para-style.

tion, more complete specimens are required to establish definitely the presence of *Hyrachyus* in Asia.

HYRACHYUS AND CHASMOTHERIUM AS HEALETID TAPIROIDS

Savage, Russell, and Louis (1966, pp. 15–16), in reviewing the affinities of *Hyrachyus*, stated, ". . . the morphologic-phyletic grade is so complete that North American *Hyrachyus* also can be described as a slightly altered, large size tapiroid" (p. 15). However, they also stated (p. 16) that my suggestion (Radinsky, 1965b, p. 234) that *Hyrachyus* should be transferred to the Tapiroidea implied that *Hyrachyus* was not ancestral to later rhinocerotoids and, apparently because they disagreed with that inference, they

concluded by retaining *Hyrachyus* in the Rhinocerotoidea. In my opinion, that inference and the taxonomic conclusion they based on it are unjustified.

I have recently (Radinsky, 1966a, pp. 631–635) discussed the phylogenetic position and taxonomic rank of *Hyrachyus*. I place *Hyrachyus* in the Tapiroidea because its molar pattern is basically that of a primitive ceratomorph, with large parastyles, unmodified metacones, and low metacolophids and paracolophids, such as are seen in primitive tapiroids like *Heptodon* and *Lophiodon* (see fig. 3). The main specialization of the dentition of *Hyrachyus* is the loss of the M_3 hypoconulid, but that also occurred independently in several tapiroid lineages. The diagnostic rhinocerotoid features of long, flat, molar metacones, reduced parastyles, and high paracolophids and metacolophids were not achieved by *Hyrachyus*, although the dentition of the late Bridgerian *H. modestus* population appears to be developing in that direction. Because *Hyrachyus* has not diverged much in dentition or other skeletal features from the primitive ceratomorph tapiroid condition, and has not achieved the dental specializations that characterize the Rhinocerotoidea, I have transferred *Hyrachyus* to the Tapiroidea, an action that implies nothing about the phylogenetic position of *Hyrachyus* relative to rhinocerotoids.

Hyrachyus is basically an enlarged but otherwise little-changed version of early representatives of *Heptodon*, a primitive helaletid tapiroid, and therefore I place *Hyrachyus* in the Helaletidae, separated from other helaletids on the subfamily level. *Hyrachyus* appears to have given rise to the early Uintan hyracodontid rhinocerotoid *Triplopus* through the late Bridgerian *Hyrachyus modestus*. *Hyrachyus eximus* may have given rise to the hyracodontid *Forstercooperia*, although intermediate forms for this transition are unknown. Finally, in Europe, *Hyrachyus minimus* appears to have given rise to *Chasmotherium cartieri*. *Chasmotherium* has been classified with *Lophiodon* in the family Lophiodontidae, recently divided into Lophiodontinae and Chasmotheriinae by Viret (1958, p. 466). However, the main reason for associating those two genera has been geographic proximity rather than any special morphologic similarity. Since *Chasmotherium* can be traced back to *Hyrachyus*, I hereby transfer the monotypic subfamily Chasmotheriinae to the Helaletidae. My interpretation of helaletid phylogeny is presented in figure 4.

SUMMARY

The rhinocerotoid family Hyrachyidae, which in its last review (Wood, 1934) included four genera and 12 species, is reduced to a subfamily, with one genus and three species, and included in the tapiroid family

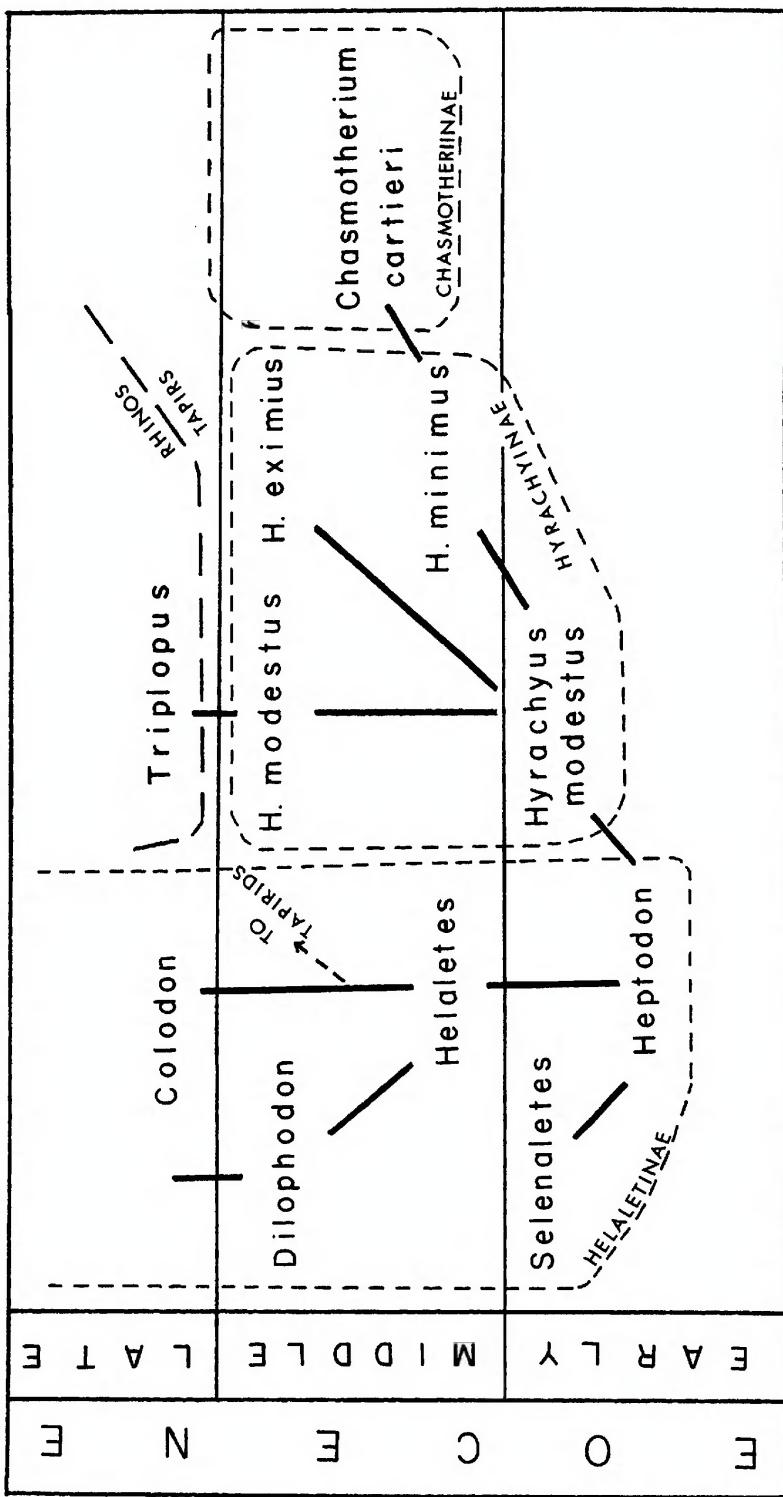


FIG. 4. Suggested phylogeny of Eocene heloletid tapiroids. *Hyrachys modestus* appears to have given rise to the primitive hyracodontid rhinocerotoid *Triplopus*; other early rhinocerotoids, such as *Forstercoptaria* and *Anyndon*, were probably derived from other tapiroid species.

Helaletidae. Because the European genus *Chasmotherium* can be traced back to *Hyrachyus* [via the lineage *Hyrachyus modestus* (=*H. "stehlini"*)-*Hyrachyus minimus*-*Chasmotherium cartieri*], the monotypic subfamily Chasmotheriinae is transferred to the Helaletidae. A synopsis of the taxonomy follows.

SUPERFAMILY TAPIROIDEA GILL, 1872

FAMILY HELALETIDAE OSBORN, 1892

SUBFAMILY HELALETINAE OSBORN, 1892

DIAGNOSIS: Helaletids characterized by a trend toward increasing bilophodonty (by lingual depression and shortening of metacones and reduction of metalophids) and development of a proboscis (inferred from the enlargement of the nasal incision and reduction of nasals). Incisors spatulate. Postcanine diastema present. P_1 lost early; other premolars non-molariform to submolariform. M_3 with or without a small hypoconulid. Included genera: *Heptodon*, *Selenaletes*, *Helaletes*, *Dilophodon*, and *Colodon* (for discussion, see Radinsky 1963, 1965b, and 1966b).

SUBFAMILY HYRACHYINAE OSBORN, 1892 (NEW ASSIGNMENT)

DIAGNOSIS: A conservative group preserving into the Middle Eocene primitive dental and skeletal features seen in the earliest *Heptodon*. Incisors spatulate. Postcanine diastema present. P_1 retained; premolars non-molariform to submolariform. No tendency toward bilophodonty. M_3 without a hypoconulid. No nasal incision enlargement. Sole genus: *Hyrachyus*.

HYRACHYUS LEIDY, 1871

TYPE SPECIES: *Hyrachyus modestus* (Leidy), 1870.

INCLUDED SPECIES: Type and *H. eximus* Leidy, 1871, and *H. minimus* (Fischer), 1829.

DIAGNOSIS: Same as for the subfamily.

Hyrachyus modestus (Leidy), 1870

Lophiodon modestus LEIDY, 1870.

Hyrachyus agrestis LEIDY, 1871.

Lophiodon bairdianus MARSH, 1871.

Lophiodon affinus MARSH, 1871.

Colonoceras agrestis: MARSH, 1873.

Hyrachyus crassidens OSBORN, SCOTT, AND SPIER, 1878.

Chasmotherium stehlini DEPERET, 1904.

Metahyrachyus bicornutus TROXELL, 1922.

Ephyrachys cristalophus WOOD, 1934.

Chasmothereum minimum (in part): FISCHER, 1964.

TYPE: U.S.N.M. No. 661, an isolated DP³ or DP⁴ from Bridger B beds, Bridger Basin, Wyoming.

KNOWN DISTRIBUTION: Late Early Eocene to Middle Eocene of North America; Cuisian (=late) Early Eocene of Europe.

DIAGNOSIS: A small to medium-sized *Hyrachys* species: mean length of M¹⁻³ from about 45 to 50 mm. (see tables 1, 2, 4). Premolars non-molariform. Upper molars usually lack lingual and labial cingula.

Hyrachys eximus Leidy, 1871

Hyrachys princeps MARSH, 1872.

Hyrachys imperialis OSBORN, SCOTT, AND SPIER, 1878.

Hyrachys hypostylus WOOD, 1934.

Metahyrachys troxelli WOOD, 1934.

TYPE: A.N.S.P. No. 10320, P₄-M₁, from Bridger C or D beds, Bridger Basin, Wyoming.

KNOWN DISTRIBUTION: Late Middle Eocene of North America.

DIAGNOSIS: Size large: mean length of M¹⁻³, 64 mm. Premolars non-molariform. Upper molars usually lack lingual and labial cingula.

Hyrachys minimus (Fischer), 1829

Lophiodon minimum FISCHER, 1829.

Hyrachys intermedius FILHOL, 1888.

Chasmothereum minimum DEPERET, 1904.

Hyrachys minimus SAVAGE, RUSSELL, AND LOUIS, 1966.

TYPE: None designated.

RANGE: Early Middle Eocene of Europe.

DIAGNOSIS: A medium-sized *Hyrachys* species: mean length of M¹⁻³, about 50 mm. Premolars submolariform. Upper molars usually with labial and lingual cingula. M³ metacone situated more labially than in other *Hyrachys* species. In these features *H. minimus* is intermediate between other *Hyrachys* species and *Chasmothereum cartieri*.

SUBFAMILY CHASMOTHERIINAE VIRET, 1958 (NEW ASSIGNMENT)

DIAGNOSIS: Aberrant helaletids with conical incisors, no postcanine diastema, and precociously molariform premolars. P₁ retained. M¹⁻² retain primitively long and labially situated metacones; M³ metacone displaced labially. M₃ without a hypoconulid.

SOLE GENUS AND SPECIES: *Chasmothereum cartieri* Rütimeyer, 1862.

RANGE: Middle Eocene and early Late Eocene of Europe.

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